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THE ROLE OF FIRE AND NITROGEN ON PLANT INVASION INTO SAGEBRUSH STEPPE

The Role of Fire and Nitrogen on Plant Invasion into the Sagebrush Steppe

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Final Report
Grant #05-CO-11221682-179
With Montana State University / Center for Invasive Plant Management

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SUMMARY

Perturbations that increase nutrient availability can shift community dominance from native to alien species, and increased nitrogen availability has been linked to plant species invasions in sagebrush ecosystems. Nitrogen availability in sagebrush ecosystems is influenced by fire history and the presence of nitrogen fixing species, and may be increasingly affected by nitrogen deposition. The goal of this study was to investigate relationships among fire, nitrogen fixing species, and invasive species to determine if fire and or the presence of nitrogen fixing species facilitate invasion by exotic species in the sagebrush steppe.

The original intention of this project was to conduct the survey in the Northeastern Sierra Nevada. However, due to an inability to locate the necessary sites, the study was conducted in the sagebrush steppe of the Central Great Basin. A Joint Fire Sciences Project Demonstration Area that is located in this region proved to be an ideal site for this survey because it provided the unique situation of having multiple, established blocks of control and burn areas within close proximity to one another. Although the ecosystem is slightly different, similar smaller surveys within the sagebrush steppe of the NE Sierra Nevada suggest that the patterns observed within the Great Basin are consistent throughout the sagebrush steppe range. Future studies will therefore investigate the role of nitrogen fixing lupines in the NE Sierra Nevada.

This study indicates a number of patterns that deserve further investigation. As is seen in other systems, within the sagebrush steppe, lupines increase after fire. However, unlike many other ecosystems, lupines remain a large component of the community even in undisturbed areas. This suggests that they may play a more influential role throughout development and maintenance of the community and not just at the early stages post disturbance. Further, the role of lupines may change depending on time since disturbance an ' site conditions. Relationships between lupine cover and amounts of available soil inorganic N and cover different functional groups varied depending on the fire treatment, and the potential facilitory effects of lupine presence appeared greatest in the non-burned sites. Although the cover of the exotic annual *Bromus tectorum* remained relatively low at this site, the data supports the idea that its expansion is promoted by fire, and suggests that under certain conditions it may also be promoted by lupine presence. The high nitrogen content and low C:N ratio of lupine litter suggest that this species undergoes rapid decomposition and contributes to more rapid mineralization of nitrogen. This could be one possible mechanism that may facilitate establishment and growth of other plant community species.

Future work will further investigate how lupines may be influencing the resource availability and how the resource environment may in turn be influencing this functional role. In addition, studies will be conducted to determine if lupines modify competitive interactions by influencing resource availability. Lastly, a manipulative field experiment will be conducted to clarify the potential mechanisms by which lupines may modify the resource environment, how lupines influence seedling establishment and survival, and if native and exotic species respond similarly to lupine resource modifications.

INTRODUCTION

The widespread occurrence of invasive species has brought new awareness to processes controlling community composition and invasion events. In sagebrush ecosystems, soil nutrients, particularly nitrogen, are often limiting. This arguably makes resource availability a primary factor determining invasion success (see Davis et al. 2000). Disturbances such as overgrazing and fire are common and have important effects on both resources and species interactions (Johnson et al. 1998, Blank and Young 2004). In semi-arid systems, fire can result in a pulse of available nitrogen that can remain elevated for two or more years (Blank et al. 1994, Rau et al. submitted). Nitrogen-fixing species are often abundant in nitrogen poor systems and can alter both resource cycling and availability (e.g. Maron and Connors 1996, Yelenik et al. 2004, Vitousek and Walker 1989), especially after fire (Johnson et al. 1998). Addition of nutrient rich litter from nitrogen fixing plants can create pockets of high soil fertility that may promote invasion after the death of the nitrogen fixer (e.g. Maron and Connors 1996).

Although common in cold deserts, little is known about the role of legumes in this ecosystem. Legumes such as lupines can make up a large component of sagebrush systems, especially after fires (Dhaemers 2006). Although populations of lupines decrease in infrequently burned areas, they are still dominant species on the landscape. Prior work suggests that amounts of nitrogen fixed by lupines can be substantial (Johnson and Rumbaugh 1981, Kenny and Cuany 1990, Rumbaugh and Johnson 1991), but the role of lupines and their contribution of nitrogen to the system via symbiotic fixation is not well understood. The combination of response to fire and ability to persist in developed communities suggest that lupines may be a critical component affecting nutrient availability in both disturbed and undisturbed areas.

In these resource-limited communities, increased nitrogen availability from fire and symbiotic fixation, could shift community dominance from native to alien species. The most common invader in these systems is the annual grass *Bromus tectorum* (cheatgrass), which increases in abundance after fire and which can, in turn, increase the frequency of fire (D'Antonio and Vitousek 1992). Cheatgrass benefits from nitrogen addition and can be an effective competitor for limited nutrients (Melgoza et al. 1990, Monaco et al. 2003, Lowe et al. 2002). More recently, aggressive perennial composites like yellow star thistle, *Centaurea solstitialis,* and several of the knapweeds, e.g, *Centaurea diffusa* and *Centaurea squarrosa*, are also expanding into the region. Their behavior in montane habitats elsewhere suggests that they could eventually become invasive in these environments. Therefore, understanding the role of fire and the nitrogen contribution of *Lupinus argenteus* will increase our understanding of nitrogen availability in sagebrush systems and its implications for invasion events.

IMMEDIATE RESEARCH OBJECTIVES

The objectives of this study were to:

1. Quantify community composition and productivity along paired burned and control transects.
2. Determine if changes in productivity of nitrogen fixing species and non-native species occur following burning.
3. Identify species associations with nitrogen fixing species on burned and control plots.
4. Determine if non-native invaders have a higher probability of association with nitrogen fixing species and if these associations change after fire.

Differences in the timing, amounts and sources of nitrogen from nitrogen fixation and fire will have distinct impacts on community composition, productivity and susceptibility to invasion. Although many ecosystems experience nitrogen input from both fire and nitrogen fixers, few studies integrate the cumulative or synergistic effect of these factors or consider which source is most influential for successful

invasion events. The results from this survey are being used to provide baseline data necessary for designing a multi-year mechanistic field experiment.

APPROACH AND METHODS

Study Area

Underdown Canyon (39°15'11" N 117°35'83"W) is located in the Shoshone Mountain Range on the Humboldt-Toiyabe National Forest (Austin Ranger District) in Nye and Lander Counties, Nevada. The mean temperature as recorded in Austin, NV ranges from -7.2°C in January to 29.4°C in July. Precipitation is mostly in the form of snow or spring rains, with mean annual amounts ranging from 23cm at the bottom to 50cm at the top of the drainage. Alluvial soils with generally halomorphic characteristics dominate the site and soil depths vary to more than a meter in vegetated areas.

This canyon is the site of many manipulative management experiments and has been used as a demonstration area to investigate the effects of prescribed fire on restoration. In the spring of 2002, 4 separate controlled burns were conducted by the Humboldt-Toiyabe and BLM fire crews, using standard methods, on north facing alluvial fans along an elevational gradient from 2073 to 2225m. Adjacent to each burn was a paired control site. In the spring of 2004, another series of controlled burns were conducted along the same gradient in close proximity to the prior control/burn pairs. Therefore, this canyon provides the unique situation of having multiple, established blocks of control, 2002 burn and 2004 burn areas within close proximity to one another that span an elevational gradient. In this study, we surveyed three of these pairs across a 265m elevational range.

Experimental Design

The study was a complete randomized block design with subsampling. Three replicate blocks were established in Underdown Canyon. Each block contained three treatments 1) an unburned control 2) an area that was burned in 2002 and 3) an area that was burned in 2004. All blocks were characterized by similar soils. Aspects were predominantly north-facing and slopes ranged from 5 to 15%. The 3 blocks spanned an elevational gradient of 2073 to 2195m.

For each treatment block, factors related to lupine abundance, nutrient contribution, and community composition and productivity were recorded using a restricted random sampling design. Within each block, two 50 m transects were set up in areas with similar vegetation, soils, and elevation on each of the three treatments. Transects were placed 25m apart. Location of the first plot on each transect was randomly assigned and remaining plots were located every 2 meters along the transect. Plots were surveyed by placing a $1m^2$ quadrat on the upslope side of the transect line.

To determine if lupines within the sagebrush steppe are altering available soil nutrients, a soil sample was also collected from the biomass plots to determine if available soil nitrogen is related to lupine presence/absence. The soil samples were taken from the center of the subplot to a depth of 10cm. Samples were homogenized, air dried, and sieved to remove particles >2mm. Inorganic N in a 10g subsample was extracted using 2.0M KCl to obtain concentrations of NH_4 and NO_3.

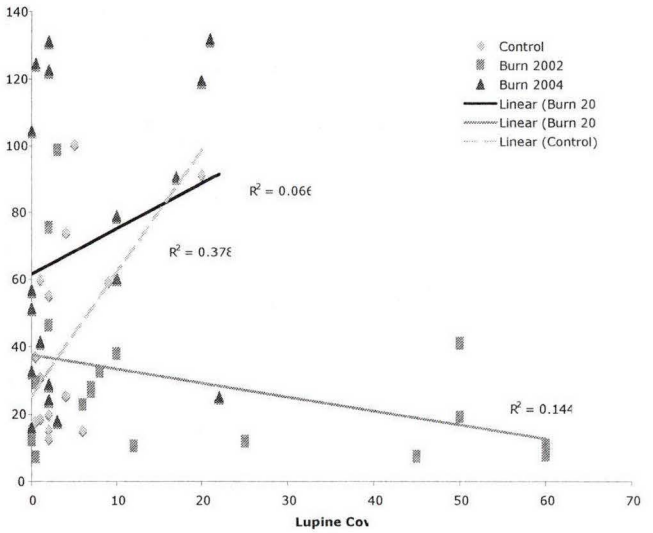
To determine the density and size distribution of lupines in this sagebrush system and any differences relating to fire or time since fire, the number of lupines within each $1m^2$ plot and the basal diameter within a subset of plots was recorded. To investigate the effect of fire and symbiotic nitrogen fixation on community composition and productivity, ocular aerial estimation of the percent cover of all functional groups (annual grass or forb, perennial grass or forb, shrub, lupine, other nitrogen fixers) present within t $1m^2$ plot was performed. In addition, biomass was clipped in a randomly selected subsample of the plots

to examine the effect of fire and fixation on productivity. Within these quadrats, biomass was clipped to the ground, sorted by functional group, and taken back to the lab where it was dried at 35°C for 48h and weighed. In addition, all species present within the biomass plots were identified to species to determine if there are consistent species associations around lupine perimeters or if there is a difference in species diversity in patches with and without lupines. A subsample of biomass tissue was also analyzed for N and C content to determine treatment and lupine presence effects on tissue concentrations.

PROJECT RESULTS

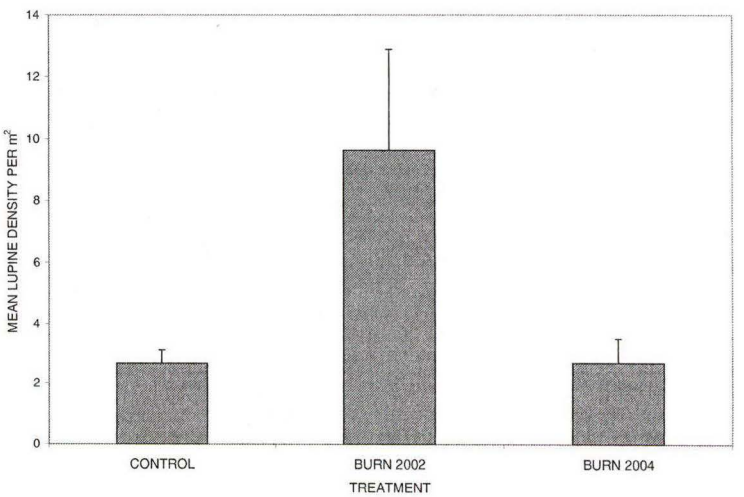
Soil Nitrogen

The amount of available inorganic N varied by treatment, with the sites burned in 2004 having the largest amounts of both NH_4 and NO_3 and the 2002 burned sites having the least, although differences among treatments were not significant. The large variability among sites could be a result of microsite effects related to the recent fire. The relationship between available soil inorganic N and lupine cover also varied by treatment (Figure 1). Control plots showed the strongest positive relationship between lupine cover and available soil inorganic N. A similar response was also observed in the 2004 burn treatment. In contrast, there was a slight negative relationship between lupine cover and soil inorganic N on the 2002 burn sites. A similar relationship is observed for lupine biomass and soil inorganic N among the three different treatments.



Lupine density, cover, and size distribution

Although overall treatment effect on lupine density was only marginally significant, ($F_{2,4} = 6.32$, $p=0.058$), mean comparisons indicate that the 2002 burn was significantly different from the other two treatments. Lupine density was greatest on the sites burned in 2002, with an average of 4 times more lupines per plot than on the control ($p=0.041$) or recently burned sites ($p=0.034$) (Figure 2). This is also where most seedlings were observed. This is supported by the lowest mean basal diameter for this treatment as compared to the other treatments (2.3 cm for old burn, 5.2 cm for recent burn and 3.3 cm for control), although only the old burn and new burn are significantly different ($p=0.028$). The recently burned sites had the largest mean basal diameter due to the majority of lupines being present as resprouts and the low frequency of seedlings. The control sites were intermediate in response for mean basal diameter, which reflects their more even distribution of seedlings and resprouting individuals.



Although the mean basal diameter was lowest on sites burned in 2002, these sites also had some of the largest resprouting lupines surveyed (maximum diameter of 28 cm for 2002 burn sites, 20 cm for 2004 burn sites, and 12 cm for control sites). Sites burned in 2002 had the largest amount of lupine cover followed by

the sites burned in 2004 and lastly the control sites, where only 3% of lupines surveyed had a diameter of 10cm or greater. Due to variability among the treatments, only marginally significant differences in cover existed between the control and 2002 burned sites (p=0.084).

Tissue chemistry

Concentration of total carbon and nitrogen in lupine tissue was not significantly different among treatments (Table 1). Significantly higher amounts of both carbon and nitrogen content occurred on the 2002 burn sites because of large differences in biomass production among the different treatments. A similar patter was seen for lupine tissue P concentrations and content (Table 1). There were no significant differences in carbon concentrations for *Poa* tissue among the treatments. However, tissue N concentrations did differ by treatment, with plants collected from the 2004 burn sites containing almost twice as much N as from the control and 2002 burn sites (Table 1). Although there were no differences in tissue N concentrations between the control and 2002 burn sites, the pattern of tissue N concentration followed that of available soil N. As was seen for lupines, differences in biomass among the treatments are reflected in the different contents of C and N among sites (Table 1).

Table1. Mean tissue concentrations and content of C, N, and P for lupine and C and N tissue concentrations and content for *Poa* for each treatment.

Treatment	Species	Carbon Concen. ($^{-1}$	Carbon Content m^{-2}	Nitrogen Concen. $^{-1}$)	Nitrogen Content m^{-2}	Phosphorous Concen. $^{-1}$	Phosphorous Content (m^{-2})
Control	Lupine	0.445	14.67	0.0293	0.92	0.00255	0.07
	Poa	0.421	9.23	0.0126	0.24		
Burn 2002	Lupine	0.447	121.08	0.0279	7.39	0.00244	0.67
	Poa	0.431	23.75	0.0121	0.58		
Burn 2004	Lupine	0.444	58.63	0.0264	3.69	0.00247	0.33
	Poa	0.423	5.20	0.0224	0.28		

In comparing the two species, concentrations of tissue carbon did not differ between species, although the greater biomass production of the lupines led to greater carbon content in lupines than *Poa* for all treatments. In contrast, lupines had almost two times greater concentrations of N under all treatments except the 2004 burn. Differences in plant biomass response to the fire treatments resulted in lupines having greater N content at all sites. Lupines had a significantly lower C:N ratio than *Poa* for all sites except the 2004 burn treatment.

Community productivity

In plots without lupines, more biomass was produced on the 2002 burn sites than on the other two treatments. Separating out the biomass to the different functional groups indicates that both perennial and annual forbs increased with burns whereas perennial grasses decreased. However, these differences in biomass production are not significant due to the small number of plots lacking lupines and the large variability among plots.

In lupine present plots, more biomass also is produced on the 2002 burn sites as compared to the other treatments. Much of the difference in biomass production between the control and the two burns is due to

the increased growth of the lupines. This can be observed when lupine biomass is subtracted from the total biomass amount. Although total biomass values decrease by half or more in some treatments, the overall trend of increased biomass in the 2002 burned sites is still present. In general, this pattern seems to hold when biomass is separated by functional groups. With the exception of perennial grasses, biomass of all of the functional groups was least on control sites and most on the 2002 burned sites.

Community composition

The different functional groups responded differently to the burn treatments. Cover of shrubs was significantly lower on burned versus control plots ($p=0.034$), whereas cover of annual forbs, perennial forbs, and other nitrogen fixing species (such as *Astragalus*) did not differ among the treatments. The cover of perennial grasses did not differ between control and the 2002 burned sites, but was significantly reduced on the 2004 burned sites ($p<0.05$). The only annual grass that was encountered at Underdown was *Bromus tectorum*. The presence of this exotic, annual grass is patchy (personal observation). However, cover of this species is greater on older burned sites than on recent burned sites ($p=0.047$). The correlation between functional group cover and lupine cover also varied depending on burn treatment. For the control sites, the cover of all functional groups, with the exception of perennial grasses, showed a slight positive correlation with lupine cover (Figure 3). The opposite pattern was observed for the 2002 burn sites, where the cover of most functional groups, with the exception of perennial grasses, showed a slight negative correlation with lupine cover. Cover of all functional groups showed a positive correlation with lupine cover on the 2004 burn sites. However, for all treatments, only the correlation between lupine cover and cover of annual forbs was significant ($p<0.05$).

In addition to identifying differences in the cover of functional groups within each treatment, the species that were collected for biomass analysis were identified for both lupine present and absent plots. Although there are no differences in the species present, on average there was two times more species present in lupine present than absent plots.

DISCUSSION

At this site within the sagebrush steppe, density of lupines was greater on burned sites as compared to unburned sites. Prior work in other systems, such as the tallgrass prairie and pine forests of the southeastern US, has found similar positive responses of legumes to fire (Towne and Knapp 1996, Hendricks and Boring 1999, Newland and DeLuca 2000). Although not directly measured, observations also suggest that there is a difference in the proportion of seedlings to resprouts on the different treatments. The sites burned in 2004 mainly consisted of resprouting individuals. This could be due to harsher conditions post-fire that are not favorable for seedling establishment. Further, there was likely high seed mortality attributable to the burn and this sampling year would be the first growing season for new seed production. In contrast, the sites burned in 2002 had the largest proportion of seedlings present. Although these sites had the greatest amount of vegetation cover, there still seems to be appropriate microsites for germination and establishment. Within these sites, there were still a few openings, but in addition, there is more availability of light due to fire-induced mortality of trees and shrubs as compared to control sites. The control appeared to have a higher number of seedlings than the 2004 burn sites, which is likely due to availability of seeds. The greater density of lupines on the older burned sites suggests that there may be a delay in fire-stimulated recruitment of lupines of more than 1 year. In southeastern pine forests, density of nitrogen fixing species was found to peak 1-2 years post-fire before declining (Hendricks and Boring 1999). Any discrepancies likely result from differences in temperature, water availability post fire, as well as germination and establishment requirement of the different nitrogen fixing species.

The presence of lupines at this site increased biomass production. Although total biomass was greater in plots containing lupines, this increase was mainly due to the size of the lupines themselves. A similar

result was observed in patches of the nitrogen fixings species *Trifolium dasyphyllum*, where biomass in *Trifolium* patches was two times greater than surrounding patches with differences due to the presence of *Trifolium* rather than differences in the biomass production of other plants (Thomas and Bowman 1998). However, unlike the *Trifolium* study, there was a significant increase in biomass of perennial grasses in th presence of lupines.

The diversity of functional groups was not affected by either treatment or the presence or absence of lupines. However, species diversity averaged two times higher in plots with lupines present than plots with lupines absent. This difference could be due in part to the fact that the majority of plots without lupines were from the 2004 burn sites, which had fewer species present initially.

Plant cover was influenced by treatment. Cover of all functional groups, with the exception of shrubs, tended to be greater on older burned sites. This is likely a result of higher resource availability in the post-fire environment (Rau 2005, Cook et al. 1994). The cover of lupines also influenced cover of all functional groups; however the strength and direction of the relationship depended upon burn treatment. Further, the differences among treatments may reflect diverse role of lupines within the varied community types. For example, if lupines are fixing their own nitrogen, the positive relationship found for most functional groups in the control sites may be due to decreased competition for soil nutrients. In contrast, the large amount of lupine cover on the 2002 burn sites likely increased resource competition among lupines and other functional groups, leading to mostly negative correlations. On the 2004 burn sites, the positive influence of lupine cover on other functional groups may be due to modification of microsite habitat rather than resource modification. Nitrogen levels were highest on this treatment, suggesting that resources are not as limiting as in the older burn or control sites. However, reduced vegetation and darkened soil can increase temperatures and reduce moisture. In this case, increased lupine cover could serve to improve conditions for germination and growth.

Our results suggest that both fire and lupine presence are associated with not only greater productivity, but also with greater amounts of available soil N. A similar result has been observed in different sites with this same species (Kenny and Cuany 1990), and in a variety of systems with a number of different nitrogen fixing species (Johnson et al. 2004, Vitousek and Walker 1989, Maron and Jefferies 1996). As in these other studies, the results of this survey imply a correlative and not causative relationship. However, results from this study suggest that there is a strong connection. For example, the tissue analysis of lupine and *Poa* suggest a causal relationship: the low C:N ratio of the lupine tissue suggests that the rate of decomposition and recycling of nutrients will generally be greater when this species is present as compared to the other dominant perennial species examined, *Poa*. Although this relationship lends support to the idea that the presence of lupines increases available soil N, the fact that tissue N concentrations in lupine did not differ by treatments is puzzling.

Numerous studies have shown that tissue nutrient concentrations increase after fire (Rau 2005, Bennett et al. 2002, Anderson and Menges 1997). In fact, a prior study at Underdown Canyon found that tissue N and P concentrations of lupine increased within one year after a prescribed fire (Rau 2005). However, in this study, only *Poa* tissue concentrations follow a pattern that resembles that of available soil N, suggesting that another mechanism is influencing tissue concentrations of N in lupines. A number of factors could account for the lack of a significant response in lupines. First, the lupine plants that were collected were not all at the same developmental stage. Nutritional requirements and competitive ability of a species can vary over time, potentially confounding any detectable relationship between tissue N concentration and fir treatment in lupines. Second, it is also possible that lupine plant N is all from fixed nitrogen, making the amount of available soil N less influential for this species. Another factor that points to the contribution o fixed nitrogen to the tissue N concentration of lupine is that although plant biomass increased significantly

on burned sites, the concentrations did not decrease. This suggests that the availability of N was not limiting. This is quite interesting as the site that had the greatest amount of biomass production for lupines (and most other functional groups) was the 2002 burn, which also had the lowest amounts of available soil N.

Regardless, the results of this study suggest that lupines have the potential to influence nitrogen availability within the sagebrush steppe, through both modification of available soil N and increased productivity. Further, the apparent independence of lupine tissue nitrogen concentrations from soil nitrogen concentrations suggests that this species may be even more important in undisturbed, low nutrient systems. Thus potential exists for this species to affect compositional change of the existing vegetation through facilitation of seedling establishment within open microsites. This ability of lupines can serve to promote stability and diversity of native species, but also may create an avenue for invasion. Further experimentation in this area is needed to gain a better understanding of the role of lupines in community composition and invasion events in sagebrush systems.

VALUE OF CIPM FUNDING AND FUTURE WORK

A critical first step for experimental studies is to first identify patterns in nature that lead to interesting questions. In this regard, the funding support from CIPM has greatly improved the direction of my future studies. By having financial support to do a preliminary study, I have refined my research questions to address areas of study where information is lacking and to more clearly define the role of nitrogen fixing lupines in the sagebrush steppe system.

Based upon patterns and correlations identified in the funded study, three additional experiments have been planned. Nodule formation and nitrogen contribution by *Lupinus argenteus* may depend on soil nutrient and water availability following disturbance such as fire. Therefore, the first study uses a greenhouse experiment to determine the effect of water stress and nutrient availability on nodule formation and nitrogen contribution by *Lupinus argenteus.* Under conditions that promote nodule formation, lupines may influence competitive interactions among species. A second greenhouse study will investigate this potential effect by growing two functionally similar grasses in the presence and absence of lupines.

In addition to altering competitive interactions, lupines may be altering community composition by facilitating or inhibiting the emergence, growth, and survival of individual species. A manipulative field experiment will investigate the effect of lupines on seedling establishment at three different levels: belowground effects, litter effects, and aboveground plant effects. This experiment will not only indicate what role lupines play in community composition and invasion, but also suggest the mechanisms by which lupines are altering the resource environment.

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Budget

Description **DIRECT COSTS**	Details	Cost
SALARIES:		
Principal investigator		
Research Associates		
Technical Assistants	A field assistant for 2 months at full time ($12/hr)	$3,840.00
Total Salaries:		
FRINGE BENEFITS:		
Principal investigator		
Research Associates		
Technical Assistants	7% fringe benefits	$268.80
Total Fringe Benefits:		
Equipment & Analyses	Tape measure, collection bags, Soil analysis and Tissue analysis	$425.00
TOTAL DIRECT COSTS:		**$4,533.80**
INDIRECT COSTS		
	10% Institutional overhead	$453.38
TOTAL PROJECT SPENDING:		**$4,987.18**